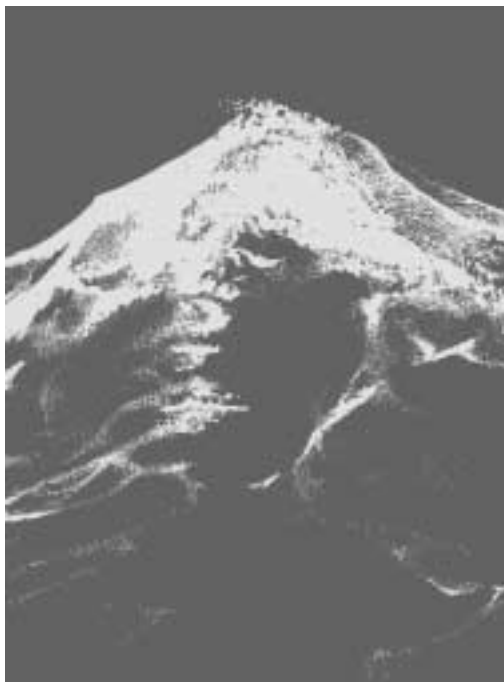


CSIRO Publishing



Marine & Freshwater Research

VOLUME 53, 2002

© CSIRO 2002

A journal for the publication of original contributions
in physical oceanography, marine chemistry,
marine and estuarine biology and limnology

All enquiries and manuscripts should be directed to:

Marine and Freshwater Research
CSIRO Publishing
PO Box 1139 (150 Oxford St)
Collingwood, Vic. 3066, Australia



CSIRO
PUBLISHING

Telephone: +61 3 9662 7618
Fax: +61 3 9662 7611
Email: publishing.mfr@csiro.au

Published by CSIRO Publishing
for CSIRO and the Australian Academy of Science

www.publish.csiro.au/journals/mfr

Validated age and growth of the dusky shark, *Carcharhinus obscurus*, from Western Australian waters

Colin A. Simpfendorfer^A, Rory B. McAuley, Justin Chidlow and Phil Unsworth

Western Australian Marine Research Laboratory, PO Box 20, North Beach, WA 6020, Australia

^APresent address and address for correspondence: Center for Shark Research, Mote Marine Laboratory, 1600 Ken Thompson Parkway, Sarasota, FL 34236, USA

Abstract. Age and growth of *Carcharhinus obscurus* was studied by vertebral ageing techniques. The annual formation of growth bands in the vertebrae was validated with oxytetracycline-injected individuals at liberty up to 1481 days. Growth-band counts of vertebral samples from 305 individuals ranging in size from 63 to 282 cm fork length were used to construct growth curves. Assuming a mean size at birth of 75.3 cm, estimates of von Bertalanffy growth parameters for males were: $L_{\infty} = 336.5$ cm and $K = 0.045$ year⁻¹. Growth parameters for females were: $L_{\infty} = 354.4$ cm and $K = 0.043$ year⁻¹. The age at maturity was estimated to be 17–22 years for females (220–250 cm), and 20–23 years for males (230–243 cm). The oldest animal aged was a 32-year-old female 274 cm in length. Growth-rate estimates based on vertebral ageing for animals up to 5 years of age are similar to those from tag-recapture studies on the same population. The results of the present study were similar to those for *C. obscurus* from the south-western Indian Ocean and the western North Atlantic Ocean, indicating that age and growth are similar among these populations.

Extra keywords: age validation, micro-radiography, elasmobranch, Indian Ocean

Introduction

The dusky shark, *Carcharhinus obscurus* (Lesueur, 1818), is a large species in the family Carcharhinidae that is distributed throughout most of the world's tropical, sub-tropical and temperate oceans (Compagno 1984). Its distribution is restricted mostly to continental shelves, but it has been reported from adjacent oceanic areas and insular shelves (Last and Stevens 1994). *Carcharhinus obscurus* is captured in fisheries throughout much of its range. In the western North Atlantic it is caught by commercial longline vessels and recreational anglers (Musick *et al.* 1993). In South Africa it is caught by recreational (Bass *et al.* 1973) and commercial (Marshall and Barnett 1997) fishers. In southern Western Australia juvenile *C. obscurus* is a target species of a shark gill-net fishery (Heald 1987; Simpfendorfer and Donohue 1998; Simpfendorfer 1999).

The life history of *C. obscurus* is considered to be one of the most K-selected of any elasmobranch. In Australian waters the young are born at a large size (70–100 cm total length (TL), Last and Stevens 1994), grow slowly (Simpfendorfer 2000), produce litters of 3–14 young every second or third year after reaching maturity (Simpfendorfer 1999) and reach a maximum size of 365 cm TL (Last and

Stevens 1994). Studies in the western North Atlantic Ocean have indicated that they mature at ~280 cm TL and 20 years of age, and live ~45 years (Natanson *et al.* 1995). These life-history parameters make *C. obscurus* extremely susceptible to over-fishing, and slow to recover from population depletion. In most situations it is considered that this species cannot be sustainably exploited by fisheries. For example, Musick *et al.* (1993) reported a 60–80% decline in the catch rates of *C. obscurus* in the western North Atlantic between 1974 and 1991. Simpfendorfer (1999), however, did demonstrate using a demographic approach that a commercial fishery in Western Australia was sustainable at its current level of exploitation because neonates were selectively targeted. This analysis was based on age and growth data from other geographic regions, making confirmation of the results dependent upon demonstrating that these parameters were the same for the Western Australian population.

Several studies of the age and growth of *C. obscurus* have been undertaken. Early attempts were undertaken in the western North Atlantic but had limited scope. Lawler (1976) estimated a von Bertalanffy growth coefficient (K , the Brody growth coefficient) of 0.014 year⁻¹ using vertebrae from only 13 females. Hoenig (1979) used vertebral samples from 22

animals to estimate that K was 0.034 year^{-1} . Schwartz (1983) examined growth using vertebrae from 34 juveniles up to 120 cm fork length (FL), and estimated that they grew $\sim 10 \text{ cm year}^{-1}$. More comprehensive work in the western North Atlantic was undertaken by Natanson *et al.* (1995) using vertebral ageing ($n = 122$) and length–frequency analysis ($n = 341$); their results indicated that K ranged between 0.038 and 0.062 year^{-1} , with most estimates close to 0.040 year^{-1} . Natanson and Kohler (1996) produced the first growth curves for *C. obscurus* outside the western North Atlantic based on 42 vertebral samples from the south-western Indian Ocean. They estimated that K was 0.047 year^{-1} . Simpfendorfer (2000) produced growth estimates of juvenile *C. obscurus* from the south-eastern Indian Ocean using tag–recapture data. He estimated that juveniles grew at average rates between 8 and 11 cm year^{-1} , but did not estimate von Bertalanffy growth parameters owing to the linear nature of growth over the size range examined.

No study of *C. obscurus* has validated the periodicity of band formation used to estimate age. In fact, age validation in the family Carcharhinidae is restricted to captive studies such as Branstetter (1987) who validated annual growth band formation in two *C. plumbeus* and seven *Rhizoprionodon terraenovae* and Wintner (2002) who examined vertebrae from ten *Carcharhinus leucas*. The only validation of growth-band formation in the wild was reported by Brown and Gruber (1988) for *Negaprion brevirostris*. Unlike other studies, periodicity of circuli formation on the vertebrae of *N. brevirostris* was validated at 29 days. Despite the limited research on the periodicity of band formation within this family a substantial portion of the shark age and growth research has been published on it.

The shark fishery in southern Western Australia uses bottom-set gill-nets to target neonate *C. obscurus* (Heald 1987). Catches over recent years have been in the order of 400–500 t, down from peak catches of $\sim 700 \text{ t}$ in the late 1980s (Simpfendorfer and Donohue 1998). Concerns over the sustainability of the *C. obscurus* stock in south-western Australia led to the implementation of a research programme that included a large tagging study, investigation of the life history, and population modelling (Simpfendorfer and Donohue 1998). As part of this study, vertebrae were collected from *C. obscurus* to determine age and growth data to enable their use in population modelling. In addition, a proportion of tagged juvenile *C. obscurus* were injected with oxytetracycline (OTC) for age validation. This paper reports the results of vertebral ageing and age validation for *C. obscurus* from the waters off Western Australia. The results are compared with those generated by Simpfendorfer (2000) using tag–recapture data, and with those from other geographic regions. The implications of the results are also discussed in relation to the validity of Simpfendorfer's (1999) assessment of the sustainability of the current levels of exploitation.

Materials and methods

Vertebral collection

Three sources of *C. obscurus* vertebrae were used. The primary method was to collect vertebral samples onboard commercial shark gill-net vessels during the course of their normal operations in south-western Western Australia. Commercial vessels used 16.5 or 17.8 cm stretch mesh gill-nets with a height of $\sim 2 \text{ m}$, and lengths between 3.5 and 7 km. Nets were demersal and set for periods from 4 to 24 h. The small mesh size of commercial gill-nets precluded the common capture of specimens longer than 120 cm FL. To obtain larger specimens, a series of research cruises along the coast of Western Australia deployed heavy set lines. Simpfendorfer *et al.* (2001) describes this fishing gear and the locations of these surveys. *Carcharhinus obscurus* specimens collected in the field (by either method) were sexed, their maturity state was determined following Bass *et al.* (1973), they were measured (FL) and a section of the anterior vertebral column was removed. Vertebrae were stored frozen until they were processed. The third source of *C. obscurus* vertebrae was a fish market where some catch from the shark gill-net fishery was sold. Specimens obtained at the fish market had been partially processed when samples were taken, and the only length measure available was partial length (PL, distance between the origin of the first dorsal fin and the dorsal origin of the caudal fin). The relationship between partial length and fork length is $[\text{FL}] = 3.31 + 1.85[\text{PL}]$ ($n = 223$, $R^2 = 0.894$), and the relationship between fork length and total length is $[\text{TL}] = 4.00 + 1.17[\text{FL}]$ ($n = 366$, $R^2 = 0.913$) (Fisheries Western Australia, unpublished data). No sex or maturity data were available for market specimens. A section of the anterior vertebral column was excised and stored frozen.

Tag–recapture study

Juvenile *C. obscurus* were tagged onboard commercial shark gill-net vessels during their normal operations off south-western Western Australia. Details of the tagging process, and the areas of release, are provided by Simpfendorfer (2000). Individuals were measured (FL), sexed and tagged with a Jumbo Rototag in the first dorsal fin. In total, 2199 tagged *C. obscurus* were released, with 879 injected with OTC (25 mg kg^{-1}) to mark the vertebral centra. Information on tag–recaptures, including date, location and fork length, and vertebral samples, were returned by commercial fishermen and research observers operating in the shark gill-net fishery.

Vertebral analysis

Vertebral samples were defrosted, excess tissue excised and individual centra separated before immersion in 5% sodium hypochlorite solution to remove any remaining flesh. Immersion time varied with the size of the centra and the age of the solution. Cleaned centra were dried in an oven at 50°C , embedded in fibreglass resin and sectioned longitudinally with a diamond-tipped blade mounted on an electric milling machine. Sections were ground on wet-and-dry paper until $\sim 0.3 \text{ mm}$ thick. Micro-radiographs were made by placing sections on top of a light-proof bag containing Agfa Structrix D4 FW scientific-grade film and exposing them in a soft X-ray machine (Hewlett-Packard 43805) at 25 kV and 2 ma for 90 s. Films were developed by standard development techniques described by the manufacturer.

Micro-radiographs were prepared for three centra for each individual and were examined under a dissecting microscope with transmitted light. Counts of the number of growth bands (defined as a transparent ring, which was dark on micro-radiographs, and the adjacent opaque ring, which was white on micro-radiographs) were made for each of the micro-radiographs from each individual. Counts of growth bands commenced after the birth mark, which was identified by a change in angle on the outer edge of the corpus calcerium and an opaque band. Counts were made without knowledge of the size, sex or

previous results for the individual. Three readers with experience in ageing elasmobranchs made counts. The consensus count for each specimen for each reader was determined by taking the count that matched in at least two of the three micro-radiographs. If counts for each of the micro-radiographs were different, that individual was excluded from analysis for that reader. The same approach was used to determine the final number of growth bands in each individual, with consensus reached between the final counts for each reader.

The index of average percentage error (IAPE) was calculated for the band counts of each reader by the method described by Beamish and Fournier (1981):

$$[\text{IAPE}] = \frac{1}{N} \sum_{j=1}^N \left(\frac{1}{R} \sum_{i=1}^R \frac{|X_{ij} - X_j|}{X_j} \right) \times 100,$$

where N is the number of animals aged, R is the number of readings done, X_{ij} is the age of the j th animal at the i th reading, and X_j is the mean age of the j th fish from i readings.

A form of the von Bertalanffy equation (Simpfendorfer *et al.* 2000) was fitted to the length-at-age data to ensure that the curve passed through the known size at birth:

$$L_T = L_0 + (L_\infty - L_0)(1 - e^{-KT}),$$

where L_0 is the size at birth, L_T is the length at time T , L_∞ is the asymptotic length, and K is the Brody growth coefficient. The size at birth used to fit the equation (75.3 cm FL for males and females) was taken from a frequency distribution given by Simpfendorfer (2000). The von Bertalanffy equation was fitted by use of the non-linear estimation module of Statistica (Statsoft, 1999).

Age validation

Vertebral samples from OTC-injected specimens were processed as for specimens for normal ageing. After X-rays were taken, sections were viewed in a fluorescent microscope using a UV filter. The distance between the centrum edge and the OTC mark was measured with an optical micrometer and the number of full growth bands (translucent and opaque pairs) between the OTC mark and centrum edge counted. To determine the periodicity of growth-band formation we calculated the slope of the regression between the number of post-OTC bands and the time at liberty (in years). The slope of the line approximates the number of bands formed per year.

Results

Validation of periodicity of band formation

Vertebrae from 34 OTC-injected *C. obscurus* were returned with tag-recapture data. Recaptured sharks were at liberty for periods from 35 to 1481 days. There was a significant linear relationship between the amount of growth after the OTC mark and the time at liberty (Fig. 1a). On average, vertebrae increased in radius by 0.6 mm year⁻¹. The numbers of growth bands formed after OTC marks were also correlated with the time at liberty (Fig. 1b). The slope of the relationship between the number of bands and the number of years at liberty was 1.20 (95% confidence interval 1.01–1.39), indicating that bands were formed approximately once each year. Individuals released in autumn (March, April or May) and recaptured after less than

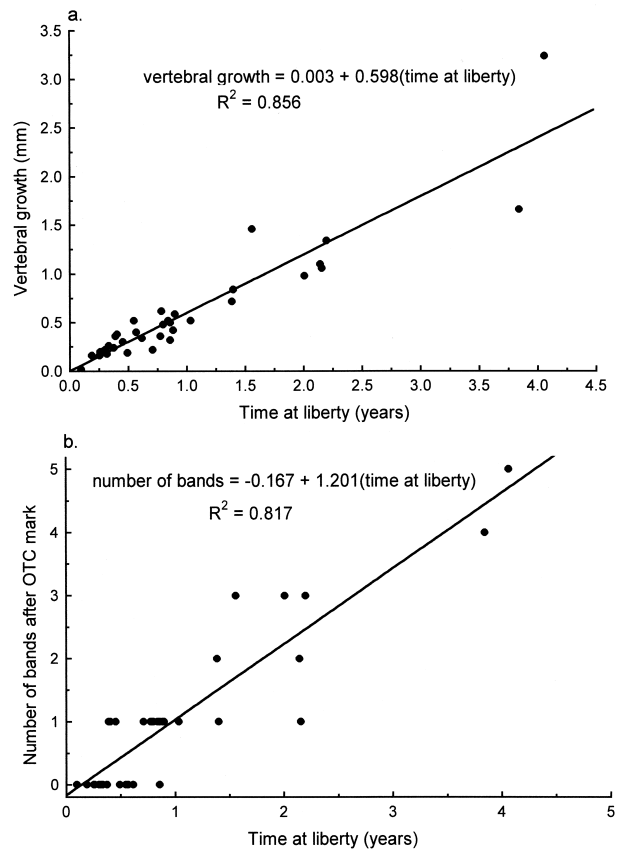


Fig. 1. (a) Growth of vertebral centra after oxytetracycline (OTC) injection, and (b) number of growth bands formed after the OTC mark, for *Carcharhinus obscurus* from Western Australia.

one year ($n = 18$) had formed a complete opaque ring (completing a growth band) if they were recaptured the following January, February or March ($n = 5$). Ten individuals recaptured before December had not formed the opaque ring. A further three animals released during winter and recaptured the following autumn had all formed an opaque ring and had a complete growth band. These data suggest that formation of the opaque band occurs during summer, mostly likely in December or January.

Age and growth estimates

Vertebrae were processed from a total of 374 *C. obscurus* ranging in size from 63 cm FL to 282 cm FL (Fig. 2). The majority of specimens were between 71 and 110 cm FL. Age estimates based on growth-band counts varied between readers. Mean band counts were similar for Readers A and B, but were considerably lower for Reader C (Table 1). The IAPEs of age estimates were lowest for Readers A and B, but approximately double for Reader C. The number of specimens for which each reader reached consensus ranged from 262 for Reader C to 358 for Reader B (Table 1). Final consensus age estimates were available for 305 specimens (82%). The mean IAPE of the final consensus counts was

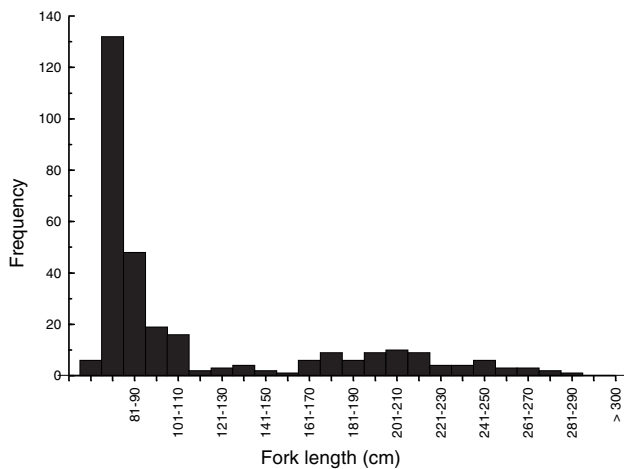


Fig. 2. Length–frequency of *Carcharhinus obscurus* specimens from Western Australia used for vertebral ageing.

Table 1. Assessment of band counts for *Carcharhinus obscurus* from south-western Australia by individual reader, and final consensus band counts
IAPE, index of average percentage error

Reader	Mean band count	IAPE	No. consensus counts	Agreement with final band counts (%)
A	4.29	9.78	337	90.4
B	3.98	7.71	358	79.6
C	2.45	18.3	262	51.6
Final	4.32	11.7	305	—

11.7 (Table 1). Readers A and B contributed the highest proportion of counts used in the final consensus ages. The most commonly aged specimens were in the 0+ and 1+ age classes, but specimens up to 25+ years of both sexes were well represented in the sample. The oldest male aged was 25+ years, and the oldest female 32+ years. The youngest mature female was estimated to be 17+ years, with all other mature females 20+ or older. The oldest immature female was 22+ years. The youngest mature male was 20+ years, and the oldest immature male 23+ years.

Von Bertalanffy growth curves indicated that growth is relatively slow (Fig. 3; Table 2). Brody growth coefficients ranged from 0.043 year^{-1} for females, and for all specimens combined, to 0.045 year^{-1} for males. L_{∞} values varied more, with the value for males being ~18 cm FL less than for females. Standard error estimates of von Bertalanffy growth parameters (Table 2) indicated that there were no differences in the Brody growth between males and females. Annual mean growth increments based on the growth curve for the combined sexes decreased slowly over time. In the first year the annual growth increment was 11.6 cm, at age five 9.4 cm, at age ten 7.5 cm, at age twenty 4.9 cm, and at age forty 2.1 cm.

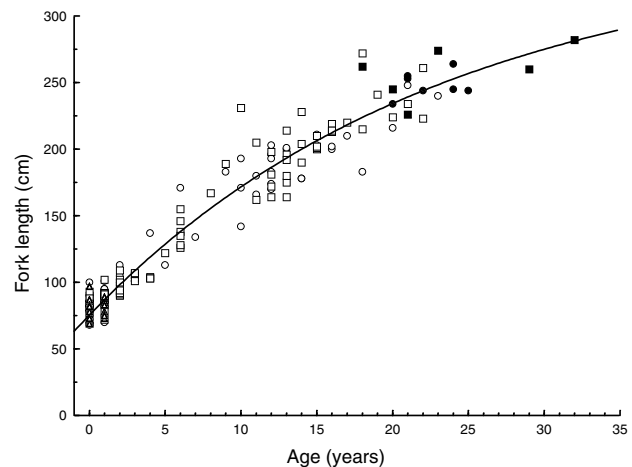


Fig. 3. Length-at-age of male (circles), female (squares) and unknown sex (triangles) *Carcharhinus obscurus* from Western Australia. Open symbols indicate immature specimens, solid symbols indicate mature specimens, and the line is the von Bertalanffy growth curve for all sexes combined.

Table 2. Estimates of von Bertalanffy parameters for *Carcharhinus obscurus* from south-western Western Australia
Values in parentheses are standard errors of parameter estimates

Parameter	Male	Female	Combined
n	111	127	305
$K (\text{year}^{-1})$	0.045 (0.007)	0.043 (0.006)	0.043 (0.005)
$L_{\infty} (\text{cm FL})$	336.5 (26.8)	354.4 (26.8)	350.8 (20.3)
R^2	0.969	0.963	0.967

Discussion

This is the first study to validate the annual formation of growth bands observed in *C. obscurus* centra. Previous studies have relied upon marginal increment analysis and comparison with length–frequency and tag–recapture data. This is also the first study to validate annual growth-band formation in the wild for a member of the genus *Carcharhinus*. Thus, more research is needed to validate age estimates across a range of species and genera within the family to increase confidence in the age and growth parameters that are already widely used in the scientific literature.

In addition to validation using OTC-injected animals, the growth rates of young *C. obscurus* estimated in this study ($10.5\text{--}10.8 \text{ cm year}^{-1}$ for age-one animals) agree closely with those estimated by Simpfendorfer (2000) using data from tag–recaptures from Western Australian waters ($9.1\text{--}10.6 \text{ cm year}^{-1}$). Previous studies have relied upon verification using length–frequency (Natanson *et al.* 1995) and marginal increments from only a few months (Natanson *et al.* 1995; Natanson and Kohler 1996). Validation in the present study was only available for animals up to five years of age. Further study will be required to validate the

Table 3. Growth parameters for *Carcharhinus obscurus* from other regions
Methods: LF, length–frequency; VA, vertebral ageing. Sex: M, male; F, female; C, sexes combined

Source	Region	Method	Sex	L_{∞} (cm FL)	K (year ⁻¹)	t_0 (years)
This study	SE Indian	VA	C	351	0.043	–
This study	SE Indian	VA	M	336	0.045	–
This study	SE Indian	VA	F	354	0.043	–
Lawler (1976)	NW Atlantic	VA	F	732	0.014	–6.7
Hoenig (1979)	NW Atlantic	VA	C	385	0.034	–5.99
Natanson <i>et al.</i> (1995)	NW Atlantic	VA	M	373	0.038	–6.28
Natanson <i>et al.</i> (1995)	NW Atlantic	VA	F	349	0.039	–7.04
Natanson <i>et al.</i> (1995)	NW Atlantic	VA	C	352	0.040	–6.43
Natanson <i>et al.</i> (1995)	NW Atlantic	LF	M	293	0.049	–5.99
Natanson <i>et al.</i> (1995)	NW Atlantic	LF	F	392	0.040	–5.34
Natanson <i>et al.</i> (1995)	NW Atlantic	LF	C	296	0.062	–4.68
Natanson and Kohler (1996)	SW Indian	VA	C	334	0.047	–5.18

periodicity of growth-band formation for older individuals. However, we hypothesize that growth-band formation occurs as an annual event at all ages.

The age and growth parameters estimated from vertebral banding patterns for *C. obscurus* in the waters off Western Australia (Table 3) are very similar to those reported from the south-west Indian Ocean (Natanson and Kohler 1996) and the western North Atlantic Ocean (Natanson *et al.* 1995). Natanson and Kohler (1996) demonstrated a statistical difference between the von Bertalanffy growth functions of the south-west Indian Ocean and western North Atlantic Ocean populations. They dismissed this difference, however, as biologically unreasonable. This result suggests that statistical comparison of the three populations is of limited value. In all cases growth was very slow, with maturity reached after ~20 years. The similarity in growth rates between regions is in contrast to some other elasmobranch species that show high variability between regions. For example, Parsons (1993) demonstrated that the bonnethead, *Sphyrna tiburo*, had significantly different growth rates between two separate localities along Florida's west coast. Branstetter *et al.* (1987) observed difference in age and growth parameters in the tiger shark, *Galeocerdo cuvier*, between the Gulf of Mexico and Virginia.

The high degree of similarity between the three populations of *C. obscurus* studied to date indicates a high degree of conservation in the life-history traits of this species. This may suggest that there is some level of genetic interchange between regions (SE Indian, SW Indian and NW Atlantic). Movements, however, between these regions would require crossing large amounts of open ocean, or an extremely circuitous route along continental shelves (SW Indian to SE Indian). Although *C. obscurus* displays patterns of migrations that cover long distances along continental shelves (Kohler *et al.* 1998), tagging studies in all three regions have not demonstrated any movements outside the normal migratory routes (Bass *et al.* 1973; Kohler *et al.* 1998; Simpfendorfer unpublished). Thus it is

unlikely that there is substantial gene flow between these three populations of *C. obscurus*. The conservative nature of the age and growth parameters is thus more likely to be a result of similar selective pressures between regions.

The growth rate of *C. obscurus* is one of the slowest in the elasmobranchs. Other members of the family Carcharhinidae that have similar values of K are *Carcharhinus brachyurus* (0.0385 year⁻¹; Walter and Ebert 1991), *Carcharhinus plumbeus* (0.046–0.089 year⁻¹; Casey *et al.* 1985; Casey and Natanson 1992; Sminkey and Musick 1995) and *Negaprion brevirostris* (0.057 year⁻¹; Brown and Gruber 1988). Other species of large carcharhinid sharks have higher values of K , including *Galeocerdo cuvier* (0.104–0.202 year⁻¹; Branstetter *et al.* 1987; Natanson *et al.* 1999; Wintner and Dudley 2000), *Prionace glauca* (0.11–0.16 year⁻¹; Stevens 1975; Skomal 1990; Tanaka *et al.* 1990), *Carcharhinus falciformis* (0.153 year⁻¹; Branstetter 1987) and *Carcharhinus longimanus* (0.075–0.103 year⁻¹; Seki *et al.* 1998; Lessa *et al.* 1999). Those large carcharhinid species that have slower growth rates tend to be those that spend some or all of their time in temperate waters and are mostly coastal, whereas those with faster growth rates tend to spend more time in tropical waters or be more open-ocean species. This suggests that temperature may play a role in determining growth rates. The exception to this is *Negaprion brevirostris*, which is slow growing but does not occur in temperate areas. Another difference that Branstetter (1990) identified between these two groups of large carcharhinid species is that the slower growing species tended to be those with protected coastal nurseries for their young, whereas the faster growing species did not have protected nursery areas. Species without protected nursery areas have a requirement to grow more quickly to avoid predation while they are young.

Although it was possible to estimate the age at maturity with a fair degree of accuracy, it was not possible to directly estimate the maximum age reached. This was a result of the small number of larger specimens obtained for this study. The oldest animal aged was a 32-year-old female. On the basis of

the observed maximum size in the present study (282 cm FL) the von Bertalanffy function suggested a maximum age of 31–34 years. Use of the maximum size for Australian waters (365 cm TL = 308 cm FL, Last and Stevens 1994) yields a maximum age of 42 years. The traditional method of estimating theoretical maximum age (95% L_{∞}) produces estimates of 60–64 years depending upon sex. These estimates, however, may be too high because the L_{∞} values are much greater than the largest observed individual (282 cm FL). Natanson *et al.* (1995) estimated a maximum age of 45 years, and Natanson and Kohler (1996) suggested a maximum age of 70 years. Both studies based these estimates on age estimates of the largest observed specimen from their respective regions. Natanson *et al.* (1995) provided tag–recapture data to support their estimates of 45 years. It is likely that Western Australian *C. obscurus* live 40 or more years, but further research needs to be undertaken to accurately determine their maximum age.

Simpfendorfer (1999) used a demographic model of the *C. obscurus* population in Western Australia and tag–recapture data to assess the impact of the catches by a commercial gill-net fishery on the intrinsic rate of population increase. The demographic model that was used relied on estimates of age at maturity and maximum age from the western North Atlantic and south-western Indian Ocean. The results of the present study confirm that the life-history parameters used by Simpfendorfer (1999) were appropriate for the analysis, and that the conclusions of the assessment – that current levels of exploitation were sustainable – are accurate.

Acknowledgments

We thank the commercial shark fishermen of Western Australia for their cooperation with this project, especially those who allowed Fisheries Western Australia staff access to their vessels for data collection and tagging, and those that returned vertebral samples with tag–recapture data. The assistance of the crew of the Research Vessel Flinders during set-line trips is gratefully acknowledged. Tony Paust, Adrian Kitchingman, Justin Bellanger, Cathy Tobin, Mark Cliff and Kevin Donohue assisted with the collection of vertebrae. We are especially grateful to Lee Higgins for her tireless work processing vertebrae. Access to X-ray facilities were generously provided by Royal Perth Hospital. This project was funded by the Fisheries Research and Development Corporation.

References

- Bass, A. J., D'Aubrey, J. D., and Kistnasamy, N. (1973). Sharks of the east coast of southern Africa. 1. The genus *Carcharhinus* (Carcharhinidae). *Oceanographic Research Institute (Durban) Investigational Report* **33**, 168 pp.
- Beamish, R. J., and Fournier, D. A. (1981). A method for comparing the precision of a set of age determinations. *Canadian Journal of Fisheries and Aquatic Sciences* **38**, 982–3.
- Branstetter, S. (1987). Age, growth and reproductive biology of the silky shark, *Carcharhinus falciformis*, and the scalloped hammerhead, *Sphyrna lewini*, from the northwestern Gulf of Mexico. *Environmental Biology of Fishes* **19**, 161–73.
- Branstetter, S. (1990). Early life-history implications of selected carcharhinoid and lamnoid sharks of the northwest Atlantic. In, 'Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics and the Status of the Fisheries'. (Eds H. L. Pratt, S. H. Gruber and T. Taniuchi.) pp. 17–28. *US Department of Commerce, NOAA Technical Report, National Marine Fisheries Service* **90**.
- Branstetter, S., Musick, J. A., and Colvocoresses, J. A. (1987). A comparison of the age and growth of the tiger shark, *Galeocerdo cuvieri*, from off Virginia and from the northwestern Gulf of Mexico. *Fishery Bulletin* **85**, 269–79.
- Brown, C. A., and Gruber, S. H. (1988). Age assessment of the lemon shark, *Negaprion brevirostris*, using tetracycline validated vertebral centra. *Copeia* **1988**, 747–53.
- Casey, J. G., and Natanson, L. J. (1992). Revised estimates of age and growth of the sandbar shark (*Carcharhinus plumbeus*) from the western North Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences* **49**, 1474–7.
- Casey, J. G., Pratt, H. L., and Stillwell, C. E. (1985). Age and growth of the sandbar shark (*Carcharhinus plumbeus*) from the western North Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences* **42**, 963–75.
- Compagno, L. J. V. (1984). FAO species catalogue. Vol. 4. Sharks of the world; an annotated and illustrated catalogue of shark species known to date. Part 2. Carcharhiniformes. *FAO Fisheries. Synopsis* **125**, 251–655.
- Heald, D. I. (1987). The commercial shark fishery in temperate waters of Western Australia. Fisheries Department of Western Australia Research Report No. 75, 71 pp.
- Hoenig, J. M. (1979). Growth rates of large sharks determined by vertebral rings. PhD Thesis, University of Rhode Island, Kingston.
- Kohler, N. E., Casey, J. G., and Turner, P. A. (1998). NMFS Cooperative Shark Tagging Program, 1962–93: an atlas of shark tag and recapture data. *Marine Fisheries Review* **60**, 1–87.
- Last, P. R., and Stevens, J. D. (1994). 'Sharks and Rays of Australia.' (CSIRO: Melbourne.) 513 pp.
- Lawler, E. F. (1976). The biology of the sandbar shark *Carcharhinus plumbeus* (Nardo, 1827) in the lower Chesapeake Bay and adjacent waters. MSc Thesis, College of William and Mary, Virginia.
- Lessa, R., Santana, F. M., and Paglerani, R. (1999). Age, growth and stock structure of the oceanic whitetip shark, *Carcharhinus longimanus*, from the southwestern equatorial Atlantic. *Fisheries Research* **42**, 21–30.
- Marshall, N. T., and Barnett, R. (1997). 'The Trade in Sharks and Shark Products in the Western Indian and Southeast Atlantic Oceans.' (Traffic East/Southern Africa: Nairobi.) 132 pp.
- Musick, J. A., Branstetter, S., and Colvocoresses, J. A. (1993). Trends in shark abundance from 1974 to 1993 for the Chesapeake Bight region of the US mid-Atlantic coast. *NOAA Technical Report, National Marine Fisheries Service* **115**, 1–18.
- Natanson, L. J., and Kohler, N. E. (1996). A preliminary estimate of age and growth of the dusky shark *Carcharhinus obscurus* from the south-west Indian Ocean, with comparison to the western North Atlantic population. *South African Journal of Marine Science* **17**, 217–24.
- Natanson, L. J., Casey, J. G., and Kohler, N. E. (1995). Age and growth estimates for the dusky shark, *Carcharhinus obscurus*, in the western North Atlantic Ocean. *Fishery Bulletin* **93**, 116–26.
- Natanson, L. J., Casey, J. G., Kohler, N. E., and Colket, T. (1999). Growth of the tiger shark, *Galeocerdo cuvieri*, in the western North

- Atlantic based on tag returns and length frequencies; and a note on the effects of tagging. *Fishery Bulletin* **97**, 944–53.
- Parsons, G. R. (1993). Age determination and growth of the bonnethead shark *Sphyrna tiburo*: a comparison of two populations. *Marine Biology* **117**, 23–31.
- Schwartz, F. J. (1983). Shark ageing methods and age estimation of scalloped hammerhead, *Sphyrna lewini*, and dusky, *Carcharhinus obscurus*, sharks based on vertebral ring counts. *NOAA Technical Report, National Marine Fisheries Service* **8**, 167–74.
- Seki, T., Taniuchi, T., Nakano, H., and Shimizu, M. (1998). Age, growth and reproduction of the oceanic whitetip shark from the Pacific Ocean. *Fisheries Science* **64**, 14–20.
- Simpfendorfer, C. A. (1999). Demographic analysis of the dusky shark fishery in south-western Australia. In 'Life in the Slow Lane. Ecology and Conservation of Long-Lived Marine Animals'. (Ed. J. A. Musick.) pp. 149–60. (American Fisheries Society Symposium No 23, Bethesda.)
- Simpfendorfer, C. A. (2000). Growth rates of juvenile dusky sharks, *Carcharhinus obscurus* (Lesueur, 1818), from southwestern Australia estimated from tag–recapture data. *Fishery Bulletin* **98**, 811–22.
- Simpfendorfer, C. A., and Donohue, K. (1998). Keeping the fish in fish and chips: research and management of the Western Australian shark fishery. *Marine and Freshwater Research* **49**, 593–600.
- Simpfendorfer, C. A., Chidlow, J., McAuley, R. B., and Unsworth, P. (2000). Age and growth of the whiskery shark, *Furgaleus macki* (Whitley, 1943), from south-western Australia. *Environmental Biology of Fishes* **58**, 335–43.
- Simpfendorfer, C. A., Goodreid, A. B., and McAuley, R. B. (2001). Size, sex and geographic variation in the diet of the tiger shark (*Galeocerdo cuvier*) in Western Australian waters. *Environmental Biology of Fishes* **61**, 37–46.
- Skomal, G. B. (1990). Age and growth of the blue shark, *Prionace glauca*, in the North Atlantic. MSc Thesis, University of Rhode Island, Kingston.
- Sminkey, T. R., and Musick, J. A. (1995). Age and growth of the sandbar shark, *Carcharhinus plumbeus*, before and after population depletion. *Copeia* **1995**, 871–83.
- Statsoft (1999). 'Statistica. Vol. I: General Conventions and Statistics I.' (Statsoft: Tulsa.)
- Stevens, J. D. (1975). Vertebral rings as a means of age determination in the blue shark (*Prionace glauca* L.). *Journal of the Marine Biological Association of the United Kingdom* **55**, 657–65.
- Tanaka, S., Cailliet, G. M., and Yudin, K. G. (1990). Differences in the growth of the blue shark, *Prionace glauca*: technique or population. In 'Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics and the Status of the Fisheries'. (Eds H. L. Pratt, S. H. Gruber and T. Taniuchi.) pp. 177–87. *US Department of Commerce, NOAA Technical Report, National Marine Fisheries Service* **90**.
- Walter, J. P., and Ebert, D. A. (1991). Preliminary estimates of age of the bronze whaler *Carcharhinus brachyurus* (Chondrichthyes : Carcharhinidae) from southern Africa, with a review of some life history parameters. *South African Journal of Marine Science*, **10**, 37–44.
- Wintner, S. P., and Dudley, S. F. J. (2000). Age and growth estimates for the tiger shark, *Galeocerdo cuvier*, from the east coast of South Africa. *Marine and Freshwater Research* **51**, 43–53.
- Wintner, S. P., Dudley, S. F. J., Kistnasamy, N., and Everett, B. (2002). Age and growth estimates for the Zambezi shark, *Carcharhinus leucas*, from the east coast of South Africa. *Marine and Freshwater Research* **53**, 557–66.

Manuscript received 21 May 2001; revised and accepted 6 September 2001